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ABSTRACT

Bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] has long been noted for poor tolerance to grazing during culm elongation in the spring. Bluebunch wheatgrass is an autoploid series of diploids (2*x*) and tetraploids (4*x*). In the mid-1980s, a group of populations were found to be allotetraploid and are now commonly referred to as Snake River wheatgrass. Relative grazing tolerance of 2*x* and 4*x* bluebunch wheatgrass and of Snake River wheatgrass is unknown. This study evaluated the effect of multiple defoliation on these grasses to simulate one consequence of grazing, removal of photosynthetic tissue. Fifteen entries representing the three taxa were established at North Logan, UT, on a Millville silt loam (coarse-silty, carbonatic, mesic Typic Rendolls; 2–4% slope) during 1988. Seedlings were vegetatively propagated into two clones apiece and transplanted adjacent to one another; one clone was subjected to multiple defoliation and the other served as an undefoliated control. Multiple defoliation at 10 cm was applied from late spring to midsummer from 1990 to 1992 at 4-wk intervals and dry matter yield was measured in late fall 1991, early spring 1992, late fall 1992, and late spring 1993. We used the defoliated-to-control ratio of plant response to estimate defoliation tolerance. The defoliated-to-control ratio for dry matter yield of Snake River wheatgrass (0.17 and 0.38 in late fall 1991 and early spring 1992, respectively) was greater than for 4*x* (0.06 and 0.18) or 2*x* (0.06 and 0.19) bluebunch wheatgrasses after the first year of multiple defoliation. The defoliated-to-control ratio for dry matter yield did not differ among taxa in late fall 1992, but the ratios for Snake River wheatgrass (0.20) and 4*x* bluebunch wheatgrass (0.21) were both greater than for 2*x* bluebunch wheatgrass (0.13) in late spring 1993. Less variation was seen among Snake River than bluebunch wheatgrass entries. Because Snake River wheatgrass had both higher yield and greater defoliation tolerance than bluebunch wheatgrass, Snake River wheatgrass is more likely to survive defoliation over the long term.

DEWEY (1984) revised the taxonomy of the perennial Triticeae on the basis of genome relationships, including realignment of the genera *Agropyron* and *Elymus*. Bluebunch wheatgrass is the only North American member of *Pseudoroegneria* (Barkworth et al., 1983), a recently recognized genus characterized by the S genome (Dewey, 1984). Bluebunch wheatgrass may be diploid ($2x = 14$) or autotetraploid ($4x = 28$), with autotetraploids occurring on more mesic sites than diploids (Carlson, 1986). Carlson (1986) also recognized an allotetraploid taxon, common in the vicinity of the Columbia, Snake, and Salmon River drainages of the Pacific Northwest. Fifty accessions of this Snake River wheatgrass have been assembled from 10 counties in Washington, Idaho, and Oregon, the only states where we know it to occur. Snake River wheatgrass is similar to bluebunch wheatgrass in its caespitose habit, general morphology, and habitat preference. The two grasses can be distinguished, however, by both vegetative and reproductive characters (Jones et al., 1991). Chromosomes of Snake River wheatgrass conform to the SH karyotype (Carlson, 1986), one of the genome combinations associated with the revised *Elymus*, and Snake River wheatgrass has been proposed as a subspecies *wawawaiensis* of *E. lanceolatus* (Scribn. & J.G. Smith) Gould.

Poor grazing tolerance coupled with high palatability has resulted in a decline in bluebunch wheatgrass since the introduction of domestic livestock to western North America grasslands. The sensitivity of bluebunch wheatgrass to grazing is well documented (Miller et al., 1986), and defoliation is a major impact of grazing. Defoliation, most detrimental at the boot stage, reduces productivity and competitiveness and increases damage with subsequent defoliation (Stoddart, 1946; Blaisdell and Pechanec, 1949; Wilson et al., 1966). These researchers reported that plants were healthier (compared with defoliation at the boot stage) when defoliated prior to elongation of reproductive tillers or during the fall. Stoddart (1946) found no yield reduction in the year following biweekly defoliation at 3 or 5 cm from 15 September to 1 November. Blaisdell and Pechanec (1949) reported no yield reduction following a single defoliation on 30 October. McLean and Wikeem (1985) reported an interaction between spring and fall defoliation; fall defoliation increased the deleterious effect of late, but not early, spring defoliation. Simultaneous drought and defoliation reduced tiller production and growth more than either treatment alone (Busso and Richards, 1995).

Considerable research has been directed at elucidating the lack of defoliation tolerance of 2*x* bluebunch wheatgrass relative to crested wheatgrass [*Agropyron desertorum* (Fisch. ex Link) Schult.]. Regrowth following defoliation is primarily driven by current (de novo) photosynthates rather than storage carbohydrates in both species (Richards and Caldwell, 1985; Busso et al., 1990). Poor initiation of tillers from axillary buds limits de novo photosynthate production in bluebunch wheatgrass. Even though sufficient buds are present, they do not elongate to form photosynthetically active tillers following defoliation (Mueller and Richards, 1986; Busso et al., 1989). That failure to initiate tillers may be related to several unmeasured environmental and physiological factors such as temperature, quantity and quality of solar radiation, resource allocation within and between tillers, or hormones regulating root/shoot balance (Richards et al., 1988). For example, Richards (1984) showed that bluebunch wheatgrass continues root growth following defoliation, whereas crested wheatgrass curtails root growth concomitant with the growth of newly initiated tillers. Defoliated crested wheatgrass showed greater flexibility of N and carbohydrate allocation between roots and shoots than bluebunch wheatgrass, resulting in a quicker return by crested wheatgrass to the predefoliation root/shoot balance (Caldwell et al., 1981). Our objective was to compare the response of 2*x* bluebunch wheatgrass, 4*x* bluebunch wheatgrass, and

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Table 1. Heading dates in 1991 and 1992 of 15 entries of 2*x* and 4*x* bluebunch wheatgrass and Snake River wheatgrass taxa established at North Logan, UT, in 1988.

Entry	Origin	Heading date† 1991	Heading date† 1992
2*x* bluebunch wheatgrass‡			
PI 232127	Penewawa Canyon, Whitman Co., WA	52 d§	32 cd
cv. Whitmar	Whitman Co., WA	53 d	34 bc
DS 120	Wawawai, Whitman Co., WA	46 f	29 e
K24	Strevell, Box Elder Co., UT	47 f	29 e
PI 547152	New Meadows, Adams Co., ID	50 e	30 de
T40450	Scott Summit, Lander Co., NV	54 cd	32 c
4*x* bluebunch wheatgrass‡			
PI 232125	Steptoe Butte, Whitman Co., ID	50 e	34 bc
P7845	Winchester, Lewis Co., ID	56 bc	36ab
K183	Willow Springs, Tooele Co., UT	60a	37a
PI 236669	Ainsworth, BC	52 d	33 c
Snake River wheatgrass‡			
cv. Secar	Lewiston, Nez Perce Co., ID	56 b	34 bc
T40599	Silcott, Asotin Co., WA	56 b	33 bc
PI 531626	Riggins, Idaho Co., ID	56 b	33 bc
PI 531627	Riggins, Idaho Co., ID	57 b	34 bc
DS 108	Colton, Whitman Co., WA	52 d	30 de
Model r^2		0.87	0.69
Significance		**	**

** Significant at the 0.01 probability level.
† Heading date: days after 31 March.
‡ As verified by Carlson (1986).
§ Entry means followed by the same letter are not significantly different according to the Waller–Duncan *k*-ratio *t*-test (*k*-ratio = 100).

Snake River wheatgrass populations to multiple defoliation beginning at the critical boot stage.

MATERIALS AND METHODS

Fifteen populations (entries) of 2*x* bluebunch wheatgrass, 4*x* bluebunch wheatgrass, and Snake River wheatgrass (taxa) were selected from materials cytologically examined by Carlson (1986), who referred to these three taxa as diploids, autoploids, and alloploids, respectively (Table 1). These entries were evaluated at Greenville Farm in North Logan, UT, on a Millville silt loam (coarse-silty, carbonatic, mesic Typic Rendolls; 2 to 4% slope). Bluebunch wheatgrass is native to this site and grows on uncultivated land nearby. Precipitation and temperature data were collected at an official weather station about 2.5 km south of the field site.

Plots of five pairs of plants of a given entry were arranged in a randomized complete block design with six replications. Pairs consisted of vegetative propagules, one randomly designated for defoliation at 10 cm and the other as a control. In earlier work, we compared defoliated (10 cm) and control treatments of Snake River and thickspike wheatgrasses, but we did not control for genotype by vegetative propagation (Jones and Nielson, 1993). The five pairs were genetically distinct, because these grasses are cross-pollinated (Jensen et al., 1990). All 15 entries were randomized in a single experiment irrespective of taxon. All plants and groups of plants (i.e., those within pairs, pairs within plots, and plots within and between replications) were spaced 2 m apart in both directions. The outer border of the experiment consisted of plants of 'Secar' Snake River wheatgrass.

Plots were established in late April 1988 with transplants grown from seed in the greenhouse for about 3 mo. Because of drought in 1988, the plants were permitted to grow without defoliation through 1988 and 1989. Defoliation at 10 cm was applied to the designated plant of each pair once in 1990 on 20 to 21 June, but by spring 1991 no difference in productivity was apparent between defoliated and control plants. Plants in our experiment were spaced far enough apart to minimize competition. Because clipping damage to bluebunch wheatgrass can be reduced by removal of competing plants (Mueggler, 1972), we suspected that more than one defoliation per year was required to negatively impact the plants when grown in a competition-free environment. Furthermore, in 1990 we observed in a separate study that 2 yr of a single spring defoliation was only mildly deleterious (Jones and Nielson, 1993).

In 1991 and 1992, therefore, we imposed three consecutive defoliations through spring and summer. Initial defoliation of a designated plant in either year was the day that either member of a pair exserted the first spike from the boot (heading date). Plants were checked three times weekly for heading date, which was recorded as the number of days after 31 March in 1991 and 1992. Mean heading date of the 15 entries ranged from 16 to 30 May 1991 and from 29 Apr. to 7 May 1992 (Table 1). The second defoliation was made at 4 wk and the third defoliation was made at 8 wk after the initial defoliation. Control plants were not defoliated at these times. Plants were defoliated with hand-held shears for spring and summer defoliation treatments (defoliated plants only) and for all yield determinations (defoliated and control plants). Both defoliated and control plants were sickle-bar mowed in August 1991 and 1992, to initiate growth cycles for late fall yield determinations.

We measured dry matter yield of harvested regrowth (above 10 cm) from both defoliated and control plants on 21 to 31 Oct. 1991 following a uniform 10-cm mowing on 19 to 20 Aug. 1991, initial spring growth on 27 Mar. to 3 Apr. 1992, regrowth 26 Oct. to 4 Nov. 1992 following a uniform 10-cm mowing on 18 to 19 Aug. 1992, and initial spring growth on 10 to 18 May 1993. Forage was dried at 60°C. The defoliated-to-control ratio for dry matter yield was calculated as the mean of a plot's defoliated plants divided by the mean of its control plants (experimental unit). At the late spring 1993 harvest, plant basal area was estimated as $(\pi/4) \times D_1 \times D_2$, where D_1 is the longest diameter of the plant at ground level and D_2 is the longest diameter perpendicular to D_1. The defoliated-to-control ratio for plant basal area was calculated as the mean of a plot's defoliated plants divided by the mean of its control plants. The plot served as the experimental unit

Table 2. Mean monthly precipitation and temperature for 1990 to 1993 at Logan, UT. Experiment terminated in May 1993.

Month	Precipitation					Temperature				
	1990	1991	1992	1993	30-yr avg.	1990	1991	1992	1993	30-yr avg.
	mm					°C				
Apr.	43	52	8	81	52	11	7	12	7	8
May	41	79	27	59	43	12	11	17	15	13
June	45	42	24	–	39	19	18	19	–	18
July	5	15	41	–	11	24	23	21	–	23
Aug.	11	16	1	–	24	23	24	23	–	22
Sept.	21	46	20	–	27	21	17	17	–	16
Oct.	34	65	54	–	36	10	11	12	–	10

for defoliated-to-control ratio for dry matter yield and plant basal area. Defoliated-to-control ratios for dry matter yield and plant basal area were considered estimates of defoliation tolerance. Control dry matter yield and plant basal area were calculated as the mean of a plot's control plants, ignoring the defoliated plants. The control plants of the plot served as the experimental unit for control dry matter yield and plant basal area.

Traits analyzed were heading date in 1991 and 1992, control dry matter yield and defoliated-to-control ratio of dry matter yield at the four harvests, and control plant basal area and defoliated-to-control ratio of plant basal area at the final harvest. Dry matter yield and plant basal area data were subjected to a $\log_{10}$-transformation before analysis to correct for positive correlations between means and variances. Reported means were back-transformed. Heading date data were not transformed.

All 15 entries (six 2*x* bluebunch, four 4*x* bluebunch, and five Snake River wheatgrasses) were arranged in a randomized complete block design with replications as blocks. Replications were considered random and entries were considered fixed. The replication × entry effect served as the error term. Entry least-squares means were separated using the Waller–Duncan k-ratio t-test at k-ratio = 100 (Smith, 1978). To maximize the power of the test, we analyzed all entries in a single data set, but for discussion we emphasized within-taxon entry differences. For comparisons among taxa, we used the same 15-entry data set and again used the replication × entry effect as the error term. Because of unequal numbers of entries among taxa, t-tests were used to separate taxa least-squares means.

RESULTS AND DISCUSSION

Precipitation in 1990 was near normal in early summer, but low in late summer (Table 2). In 1991, precipitation was near normal in all months except May, September, and October, which were wetter than normal. The spring and summer of 1992 were dry except for the wet month of July. The last three months of the experiment's growing season (October 1992 and April and May 1993) were wetter than normal. Temperatures were near normal, except for a hot and dry April and May 1992, which probably caused heading dates to average 21 d earlier than in 1991 (Table 1). Over the entire experimental period, only three plants (one of each taxon) died because of defoliation. Thus, dry matter yield response to defoliation rather than survivorship was of primary interest.

We observed considerable variation among 2*x* bluebunch wheatgrass entries for undefoliated control dry matter yield in late fall 1991, early spring 1992, late fall 1992, and late spring 1993 and for plant basal area in late spring 1993 (Table 3). Although no entry was significantly greater than 'Whitmar' for undefoliated control dry matter yield or plant basal area, PI 232127 and DS 120 were consistently similar to Whitmar. PI 547152 was similar to Whitmar for undefoliated control dry matter yield at two of the four harvest dates and for plant basal area. Whitmar, PI 232127, and DS 120 always ranked highest for defoliated-to-control ratio for dry matter yield and plant basal area as well, while K24 was similar to Whitmar for defoliated-to-control ratio for dry matter yield at three of the four harvest dates and for plant basal area (Table 4). T40450 consistently ranked low for undefoliated control and defoliated-to-control ratio for both dry matter yield and plant basal area. Despite this disparity, heading dates of Whitmar and T40450 were similar, being the two latest 2*x* bluebunch wheatgrass entries to head in 1991 and 1992 (Table 1).

Tetraploid bluebunch wheatgrass generally exhibits a more mesic adaptation and is considerably less common than 2*x* bluebunch wheatgrass (Carlson, 1986). No cultivars of 4*x* bluebunch wheatgrass have been released. Undefoliated control dry matter yield of P7845 was lowest at all four harvests, while rankings of the other three entries varied among harvests (Table 3). Dry matter yield was not related to heading date, as P7845 was intermediate to the other entries (Table 1). PI 232125 was highest among 4*x* bluebunch wheatgrass entries for undefoliated control plant basal area (Table 3). K183 ranked highest for defoliated-to-control ratio for dry matter yield at the first two harvests but last at the final two harvests, while PI 232125's ranking increased throughout the experiment (Table 4). We found no differences among 4*x* bluebunch wheatgrass entries for defoliated-to-control ratio for plant basal area.

Variation among Snake River wheatgrass entries was smaller than for 2*x* or 4*x* bluebunch wheatgrass entries generally (Tables 1, 3, and 4). The limited geographical distribution of Snake River wheatgrass may be responsible for the small amount of variation observed relative to the widely distributed bluebunch wheatgrass. T40599 and Secar ranked last for undefoliated control dry matter yield at the early spring 1992 and late spring 1993 harvests, respectively, the only harvests where significant differences were observed (Table 3). In both cases, PI 536126 was the only entry to be significantly higher yielding than any other. Differences for defoliated-to-control ratio were observed only at the late fall 1992 harvest, where DS108 was lower than Secar, T40599, and PI 531626 (Table 4).

Table 3. Undefoliated control dry matter yield and plant basal area for 2*x* and 4*x* bluebunch wheatgrass and Snake River wheatgrass entries.

Entry	Dry matter yield				
	1991 late fall	1992 early spring	1992 late fall	1993 late spring	Plant basal area†
	g plant^{-1}				m^2 plant^{-1}
2*x* bluebunch wheatgrass					
PI 232127	93abc‡	21 f	48 cd	42 fg	0.111abc
cv. Whitmar	112a	23 ef	67abc	49 ef	0.092 bc
DS 120	93abc	26 cdef	51 bcd	52 ef	0.082 bc
K24	26 ef	9 gh	8 f	26 gh	0.047 d
PI 547152	69 cd	20 f	36 de	62 def	0.079 bc
T40450	19 f	6 h	12 f	20 h	0.040 d
4*x* bluebunch wheatgrass					
PI 232125	75 bcd	25 def	28 e	53 ef	0.151a
P7845	33 e	12 g	10 f	19 h	0.089 bc
K183	62 d	20 f	47 cde	83 bcde	0.074 c
PI 236669	98ab	20 f	50 bcd	70 cdef	0.093 bc
Snake River wheatgrass					
cv. Secar	115a	38ab	81ab	82 bcde	0.086 bc
T40599	106a	32 bcde	86a	106abcd	0.083 bc
PI 531626	99ab	44a	105a	144a	0.114ab
PI 531627	88abcd	36abc	76abc	125ab	0.098 bc
DS 108	92abcd	34abcd	89a	109abc	0.090 bc
Model r^2	0.83	0.82	0.81	0.77	0.60
Significance	**	**	**	**	**

** Entries significantly different at the 0.01 probability level.
† 1993 late spring.
‡ Means followed by the same letter are not significantly different according to the Waller–Duncan *k*-ratio *t*-test (*k*-ratio = 100).

We used *t*-tests to compare the three taxa for heading date, undefoliated control dry matter yield and plant basal area, and the defoliated-to-control ratio for dry matter yield and plant basal area. In both years, mean heading dates of 2*x* bluebunch wheatgrass entries (20 May 1991, 1 May 1992) were significantly ($P < 0.01$) earlier than for 4*x* bluebunch wheatgrass (24 May 1991, 4 May 1992) or Snake River wheatgrass (25 May 1991, 3 May 1992), but the differences were small. Differences within taxa for heading date were generally as large as or larger than differences between taxa (Table 1). Rankings for defoliated-to-control ratio at the last two harvests, which followed an additional year of multiple defoliation, differed from the first two harvests. In the late fall 1991 and early spring 1992 harvests, defoliated-to-control ratio for Snake River wheatgrass was greater than for 2*x* or 4*x* bluebunch wheatgrasses, which were similar (Table 5). At the late fall 1992 harvest, however,

Table 4. Defoliated-to-control ratio for dry matter yield and plant basal area for 2*x* and 4*x* bluebunch wheatgrass and Snake River wheatgrass entries.

Entry	Defoliated-to-control ratio				
	Dry matter yield				
	1991 late fall	1992 early spring	1992 late fall	1993 late spring	Plant basal area†
2*x* bluebunch wheatgrass					
PI 232127	0.12abc‡	0.33a	0.17abc	0.25ab	0.48abc
cv. Whitmar	0.09 bcde	0.31ab	0.19ab	0.19 bc	0.54abc
DS 120	0.07 cdef	0.33a	0.15 bcde	0.19 bc	0.61a
K24	0.08 bcdef	0.14 d	0.18abc	0.16 bcd	0.55ab
PI 547152	0.05 ef	0.16 cd	0.10 efg	0.11 d	0.41 bc
T40450	0.02 g	0.07 e	0.01 h	0.03 e	0.38 c
4*x* bluebunch wheatgrass					
PI 232125	0.06 def	0.19 bcd	0.24a	0.31a	0.59ab
P7845	0.06 def	0.13 d	0.22a	0.23abc	0.68a
K183	0.10abcd	0.25abc	0.08 fg	0.16 cd	0.67a
PI 236669	0.04 f	0.16 cd	0.11 cdef	0.18 bc	0.60ab
Snake River wheatgrass					
cv. Secar	0.19a	0.35a	0.16abcd	0.21abc	0.60a
T40599	0.18a	0.41a	0.16abcd	0.23abc	0.60a
PI 531626	0.16ab	0.39a	0.13 bcdef	0.24abc	0.60a
PI 531627	0.15ab	0.38a	0.10 defg	0.16 bcd	0.60ab
DS 108	0.16ab	0.34a	0.07 g	0.18 bc	0.52abc
Model r^2	0.64	0.67	0.75	0.71	0.44
Significance	**	**	**	**	*

*,** Entries significantly different at the 0.05 and 0.01 probability levels, respectively.
† 1993 late spring.
‡ Means followed by the same letter are not significantly different according to the Waller–Duncan *k*-ratio *t*-test (*k*-ratio = 100).

Table 5. Undefoliated control and defoliated-to-control ratio for dry matter yield and plant basal area for Snake River (SRWG), 4*x* bluebunch (BBWG 4*x*), and 2*x* bluebunch (BBWG 2*x*) wheatgrass taxa.

Taxon	Dry matter yield: 1991 late fall	1992 early spring	1992 late fall	1993 late spring	Plant basal area†
Undefoliated control, g plant^{-1}					
SRWG	100a‡	37a	87a	111a	0.093a
BBWG 4*x*	62b	19b	29b	49b	0.098a
BBWG 2*x*	57b	16b	29b	39b	0.071b
Model r^2	0.83	0.82	0.81	0.77	0.60
Significance	**	**	**	**	*
Defoliated-to-control ratio					
SRWG	0.17a	0.38a	0.12	0.20a	0.58a
BBWG 4*x*	0.06b	0.18b	0.15	0.21a	0.63a
BBWG 2*x*	0.06b	0.19b	0.10	0.13b	0.49b
Model r^2	0.64	0.67	0.75	0.71	0.44
Significance	**	**	NS	**	**

*,** Taxa significantly different at the 0.05 and 0.01 levels, respectively.

† 1993 late spring.

‡ Means followed by the same letter are not significantly different according to a *t*-test at $P < 0.01$.

taxa were similar for defoliated-to-control ratio, and at the late spring 1993 harvest Snake River wheatgrass and 4*x* bluebunch wheatgrass both exceeded 2*x* bluebunch wheatgrass for defoliated-to-control ratio for both dry matter yield and plant basal area.

At all four harvests, 2*x* and 4*x* bluebunch wheatgrasses were similar for undefoliated control dry matter yield (Table 5). Their yields were only 60, 47, 33, and 40% of Snake River wheatgrass at the four harvests, respectively. Except at the first harvest, only once (K183 at the final harvest) did any bluebunch wheatgrass entry exceed any Snake River wheatgrass entry in undefoliated control dry matter yield. The Snake River wheatgrass taxon exhibited greater production when undefoliated, as well as a defoliated-to-control ratio equal to or greater than that of 2*x* or 4*x* bluebunch wheatgrasses. This resulted in Snake River wheatgrass productivity superior to 2*x* or 4*x* bluebunch wheatgrass when defoliated.

Snake River wheatgrass is a productive bunchgrass with considerable potential for rangeland seedings. Previous findings (Jones and Nielson, 1993) indicate that Snake River wheatgrass is more susceptible to reduced productivity from spring defoliation than its close rhizomatous relative, thickspike wheatgrass (*E. lanceolatus* subsp. *lanceolatus*). While Snake River wheatgrass does not possess thickspike wheatgrass's degree of defoliation tolerance, Snake River wheatgrass remained more productive under this study's defoliation regime than bluebunch wheatgrass, especially the more common 2*x* taxon. An important attribute of Snake River wheatgrass is its ease of hybridization with thickspike wheatgrass, forming partially fertile heterotic populations (Jones et al., 1995). Backcrosses of Snake River wheatgrass × thickspike wheatgrass populations to Snake River wheatgrass should generate sufficient variation to improve defoliation tolerance of Snake River wheatgrass and achieve adequate seed fertility.

While the mechanisms of defoliation tolerance in 2*x* bluebunch wheatgrass have been well studied, those of Snake River wheatgrass and thickspike wheatgrass have yet to be clarified. Thickspike wheatgrass is able to produce de novo photosynthates after defoliation at the reproductive phase because of residual leaf area below defoliation height (Jones and Nielson, 1993). This is explained in part by thickspike wheatgrass's high frequency of vegetative tillers, typically associated with a rhizomatous growth habit. However, additional factors such as synchrony of tillering, ability to tiller after defoliation, apical meristem placement, cessation of root growth upon reproductive tiller elongation, and leaf elongation rate should be investigated as factors affecting defoliation tolerance of Snake River wheatgrass and thickspike wheatgrass.

REFERENCES

Barkworth, M.E., D.R. Dewey, and R.J. Atkins. 1983. New generic concepts in the Triticeae of the Intermountain Region: Key and comments. Great Basin Nat. 43:561–572.

Blaisdell, J.P., and J.F. Pechanec. 1949. Effects of herbage removed at various dates on vigor of bluebunch wheatgrass and arrowleaf balsamroot. Ecology 30:298–305.

Busso, C.A., R.J. Mueller, and J.H. Richards. 1989. Effects of drought and defoliation on bud viability in two caespitose grasses. Ann. Bot. (London) 63:477–485.

Busso, C.A., and J.H. Richards. 1995. Drought and clipping effects on tiller demography and growth of two tussock grasses in Utah. J. Arid Environ. 29:239–251.

Busso, C.A., J.H. Richards, and N.J. Chatterton. 1990. Nonstructural carbohydrates and spring regrowth of two cool-season grasses: Interaction of drought and clipping. J. Range Manage. 43:336–343.

Caldwell, M.M., J.H. Richards, D.A. Johnson, R.S. Nowak, and R.S. Dzurec. 1981. Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia (Berlin) 50:14–24.

Carlson, J.R. 1986. A study of morphological variation within *Pseudoroegneria spicata* (Pursh) A. Löve (Poaceae:Triticeae). M.S. thesis. Oregon State Univ., Corvallis.

Dewey, D.R. 1984. The genomic system of classification as a guide to intergeneric hybridization with the perennial Triticeae. p. 209–279. *In* J.P. Gustafson (ed.) Gene manipulation in plant improvement. Plenum Press, New York.

Jensen, K.B., Y.F. Zhang, and D.R. Dewey. 1990. Mode of pollination of perennial species of the Triticeae in relation to genomically defined genera. Can. J. Plant Sci. 70:215–225.

Jones, T.A., and D.C. Nielson. 1993. Spring-clipping response in Snake River and thickspike wheatgrasses. Agron. J. 85:94–97.

Jones, T.A., D.C. Nielson, and J.R. Carlson. 1991. Developing a grazing-tolerant native grass for bluebunch wheatgrass sites. Rangelands 13:147–150.

Jones, T.A., R.R-C. Wang, and L-H. Li. 1995. Meiotic stability of intersubspecific hybrids of Snake River × thickspike wheatgrasses. Crop Sci. 35:962–964.

McLean, A., and S. Wikeem. 1985. Influence of season and intensity of defoliation on bluebunch wheatgrass survival and vigor in southern British Columbia. J. Range Manage. 38:21-26.

Miller, R.F., J.M. Seufert, and M.R. Haferkamp. 1986. The ecology and management of bluebunch wheatgrass (*Agropyron spicatum*): A review. Oreg. Agric. Exp. Stn. Bull. 669.

Mueller, R.J., and J.H. Richards. 1986. Morphological analysis of tillering in *Agropyron spicatum* and *Agropyron desertorum*. Ann. Bot. (London) 58:911–921.

Mueggler, W.F. 1972. Influence of competition on the response of bluebunch wheatgrass to clipping. J. Range Manage. 25:88–92.

Richards, J.H. 1984. Root growth response to defoliation in two *Agropyron* bunchgrasses: Field observations with an improved root periscope. Oecologia (Berlin) 64:21–25.

Richards, J.H., and M.M. Caldwell. 1985. Soluble carbohydrates, concurrent photosynthesis, and efficiency in regrowth following defoliation: A field study with *Agropyron* species. J. Appl. Ecol. 22:907–920.

Richards, J.H., R.J. Mueller, and J.J. Mott. 1988. Tillering in tussock grasses in relation to defoliation and apical bud removal. Ann. Bot. (London) 62:173–179.

Smith, C.W. 1978. Bayes least significant difference: A review and comparison. Agron. J. 70:123–127.

Stoddart, L.A. 1946. Some physical and chemical responses of *Agropyron spicatum* to herbage removal at various seasons. Utah Agric. Exp. Stn. Bull. 324.

Wilson, A.M., G.A. Harris, and D.H. Gates. 1966. Cumulative effects of clipping on yield of bluebunch wheatgrass. J. Range Manage. 129:90-91.